PALYNOLOGY, PHYLOGENETIC RECONSTRUCTION, AND CLASSIFICATION OF THE AFRO-MADAGASCAN GENUS *ARISTEA* (IRIDACEAE)[1]

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ABSTRACT

Examination of the pollen grains of *Aristea* using light and scanning electron microscopy shows that this Afro-Madagascan genus of ca. 50 species is one of the palynologically most diverse genera of the family Iridaceae. Exine sculpturing ranges from reticulate to rugulate to areolate with lumina ranging from large to small. Overall size is also variable, with grains ranging from medium-sized (45–60 μm equatorial diameter) to large (70–97.5 μm equatorial diameter). Monosulcate apertures are plesiomorphic, and derived sulculate (apertural membranes obscured by masses of exine), zonasulculate, 2-zonasulculate, 3-sulcate, and spiral apertures are present in various species. Pollen characters were combined with morphological and anatomical features in a matrix and subjected to cladistic analysis. Trees obtained using successive weighting procedures were used as the basis for a revised infrageneric classification of *Aristea* in which three subgenera are recognized. Two subgenera are restricted to the winter-rainfall zone (the Cape Floristic Region) of southern Africa, and the third is dispersed widely across sub-Saharan Africa and Madagascar but is barely represented in the Cape Region. Apomorphic character states are discussed in relation to the biology of the genus, and we suggest that some derived aperture types may be adapted to the desiccating climate of the Cape Region.

Information now available on various aspects of the pollen morphology of the Afro-Madagascan genus *Aristea* indicates that it is among the most variable genera of Iridaceae (if not the most variable) as regards pollen-grain apertures and exine sculpturing. The first reports of pollen morphology in *Aristea* (Radelescu, 1970; Schulze, 1971a), using light microscopy, made it clear that the genus was unusual palynologically. More detailed study using scanning electron microscopy (SEM) of six species occurring on Madagascar (Straka & Friedrich, 1984; Goldblatt & Le Thomas, 1992a) confirmed the apertural diversity, even in this limited geographical area and with the low species diversity for the genus. With some 50 species (Weimarck, 1940; Vincent, 1985; Goldblatt, 1995a, 1995b; Goldblatt & Manning, 1997), *Aristea* is the largest of the six genera of Nivenioideae, one of four subfamilies currently recognized in Iridaceae (Goldblatt, 1990, 1993). *Aristea* is unusual in Iridaceae in having a particularly wide geographic range. It is one of only a handful of the 35 African genera

of the family that extend across all of sub-Saharan Africa, and one of only three that are shared with Madagascar, the others being *Crocosmia* (9 spp: 1 in Madagascar) and *Gladiolus* (ca. 255 spp: 8 in Madagascar), both members of subfamily Ixioideae. *Aristea* is also among the most variable genera of Iridaceae as regards fruit and seed morphology. In this paper we extend our earlier palynological survey of *Aristea* to the African species and combine the variation in pollen-grain characters with features of fruit, seeds, and other morphological structures in a cladistic analysis in order to increase our understanding of the phylogeny of the genus. The results provide valuable insights into the evolution and geographic radiation of the genus and are used to refine the infrageneric classification.

MATERIALS AND METHODS

PALYNOLOGY

Pollen samples (Table 1) of 32 of the estimated 50 species of *Aristea* were collected in the wild,

Table 1. Species of *Aristea* examined, with voucher data and pollen grain dimensions. Voucher specimens are located at MO, with additional duplicates often at NBG, P, and PRE (herbarium acronyms after Holmgren et al. (1990)); collectors are abbreviated as follows G = Goldblatt, M = Manning. Species are arranged alphabetically within the sections recognized by Weimarck (1940). *Aristea fimbriata*, unknown to Weimarck, is assigned to section *Racemosae*, where he would presumably have placed it.

Taxon	Grain size, μm	Voucher information
Section *Singulares* Weim.		
A. *singularis* Weim.	59.1 × 51.0	S. Africa, W. Cape, *Taylor 11009* (MO)
Section *Eucapsulares* Goldblatt (= sect. *Euaristea* Weim.)		
A. *angolensis* Baker	60.0 × 58.5	S. Africa, Natal, *G & M 8360; 9818; 9870*
A. *grandis* Weim.	54.3 × 51.6	S. Africa, Natal, *G & M 9857*
A. *montana* Baker	60.0 × 57.0	S. Africa, Natal, *G & M 9858*
A. *nyikensis* Baker	61.0 × 51.0	Malawi, *Bidgood et al. 1310*
A. *polycephala* Harms	51.0 × 45.0	Tanzania, *la Croix 4267*
A. *ranomafana* Goldblatt	57.7 × 40.0	Madagascar, *Malcomber 1336*
A. *schizolaena* Harv.	66.7 × 60.0	S. Africa, E. Cape, *G & M 9588*
A. *woodii* N. E. Br.	59.5 × 56.5	S. Africa, E. Transvaal, *G & M 9815; 9831*

(*A. angustifolia* Baker, *A. humbertii* H. Perr., *A. kitchingii* Baker, and *A. madagascariensis* Baker (Goldblatt & Le Thomas, 1992a) all have grains smaller than 60 μm equatorial diameter.)

Taxon	Grain size, μm	Voucher information
Section *Trilobatae* Weim.		
A. *platycephala* Baker	60.6 × 59.6	S. Africa, E. Cape, *van Wyk & Mathews 7727*
Section *Ancipites* Weim.		
A. *abyssinca* Pax	63.3 × 55.5	S. Africa, Natal, *G & M 9855*
A. *anceps* Ecklon	54.0 × 46.9	S. Africa, E. Cape, *G & M 9530*
Section *Cladocarpae* Weim.		
A. *cladocarpa* Baker	48.5 × 45.0	Madagascar, *Bosser 16695* (see also Goldblatt & Le Thomas, 1992a)
Section *Pseudaristea* Pax		
A. *biflora* Weim.	71.2 × 70.5	S. Africa, W. Cape, *Goldblatt 8898*
A. *cantharophila* Goldblatt & J. Manning	69.2 × 66.4	S. Africa, W. Cape, *G & M 10284*
A. *ecklonii* Baker	63.0 × 59.0	S. Africa, E. Cape, ex hort
A. *lugens* (L.f.) Weim.	92.2 × 81.0	S. Africa, W. Cape, *Oliver 4739*
A. *pauciflora* W. Dod.	73.5 × 63.5	S. Africa, W. Cape, *G & M 10102*
A. *pusilla* (Thunb.) Ker	59.6 × 58.5	S. Africa, W. Cape, *Bayliss 7635*
A. *simplex* Weim.	71.1 × 67.5	S. Africa, W. Cape, *G & M 9754*
A. *spiralis* (L.f.) Ker Gawl.	73.5 × 63.5	S. Africa, W. Cape, *G s.n.* (Cape Point)
A. *teretifolia* Goldblatt & J. Manning	79.3 × 77.1	S. Africa, W. Cape, *Bean 2785; Nanni s.n.*
A. sp. ? aff. *pauciflora*	81.2 × 76.2	S. Africa, Cape, *Drewe 466*
Section *Racemosae* Weim.		
A. *confusa* Goldblatt	54.0 × 51.1	S. Africa, W. Cape, *G s.n.* (Hout Bay)
A. *fimbriata* Goldblatt ined.	73.5 × 70.5	S. Africa, W. Cape, *G & M 10167*
A. *juncifolia* Baker	52.7 × 45.0	S. Africa, W. Cape, *Williams 891; Orchard 354*
A. *major* Andrews	45.0 × 42.0	S. Africa, Cape, *G s.n.* (Hout Bay)
A. *monticola* Goldblatt	54.0 × 49.5	S. Africa, W. Cape, *G & M 9476A*
A. *racemosa* Baker	52.5 × 48.0	S. Africa, Cape, *Oakes s.n.*
Section *Aristea*		
A. *africana* (L.) Hoffmsg.	95.2 × 92.2	S. Africa, W. Cape, *G & M 9352;*
	82.5 × 81.0	*G & M 9505;*
	87.0 × 83.2	*Bean 2789;*
	88.5 × 77.2	*G & M 9750*
A. *dichotoma* (Thunb.) Ker Gawl.	97.5 × 93.0	S. Africa, W. Cape, *G & M 9503; G & M 10154*
A. *glauca* Klatt	82.5 × 75.0	S. Africa, W. Cape, *G & M 9595A*
A. *oligocephala* Baker	97.5 × 85.5	S. Africa, W. Cape, *Barker 412*

fixed in FAA, and subsequently stored in 70% ethanol, or were taken from herbarium specimens in the collections at the Laboratoire de Phanérogamie, Paris (P), or the Missouri Botanical Garden, St. Louis (MO). All samples were examined under the light microscope (LM), without acetolysis, and mounted in glycerine jelly, but after rehydration of anthers in a wetting agent and subsequent washing for herbarium samples. For SEM study, non-acetolyzed rehydrated herbarium samples and spirit material were fixed in 2.5% glutaraldehyde solution, washed in a 0.1 M cacodylate buffer, then dehydrated and critical-point dried. Pollen of *Aristea* is difficult to study owing to the fragility of the exine, of which the foot layer is extremely thin. It is important to examine non-acetolyzed grains under the light microscope in the hydrated, or rehydrated, state so that the apertures can be more clearly interpreted by the presence of thickened intine. In some cases, acetolyzed grains were examined in LM to amplify our observations. Grain size (Table 1) is the average of measurements of 10 grains mounted in glycerin jelly. The terminology used is, as far as possible, in accordance with the *Glossary of Pollen and Spore Terminology* (Punt et al., 1994) and the special sulcus types described for monocots by Halbritter and Hesse (1993).

PHYLOGENETIC ANALYSIS

Aristea is relatively uniform in floral morphology, fairly diverse in the arrangement of the inflorescence units (binate rhipidia) on the flowering stem, and remarkably variable in capsule and seed morphology. The current classification of the genus into eight sections is based largely on fruit and seed characters (Weimarck, 1940). Species are, however, recognized in many instances on inflorescence characters and sometimes on the basis of vegetative features including overall size and stem compression. Using Weimarck's monograph of the genus as the primary source of morphological data, supplemented where necessary from herbarium material and new observations (Goldblatt, 1995a; Goldblatt & Manning, 1997), we have identified 24 phylogenetically informative morphological features (Appendix 1). These have been polarized exclusively using outgroup comparison. Some of the features are quantitative multistate characters that arguably should not be included in a phylogenetic analysis. We believe they do have some phylogenetic information and are readily polarized; hence we have included them. Our outgroup is a combined one, four of the remaining five genera of subfamily Nivenioideae (Goldblatt, 1990, 1993). These are the

Australasian *Patersonia* and three shrubby southern African genera, *Klattia*, *Nivenia*, and *Witsenia*. Where characters in the outgroup genera are not congruent, we determined the ancestral state by comparing the character to genera of Iridaceae outside the subfamily. A sixth genus of Nivenioideae, *Geosiris*, was not taken into consideration for character polarization because it is a highly specialized, leafless and achlorophyllous plant, most features of which have no homologue in *Aristea*.

We also included two nontraditional characters in the analysis, one from leaf anatomy and one relating to floral nectaries. The outgroup genera have leaves with strands of subepidermal sclerenchyma in the leaf margins (Rudall & Burns, 1989), but the seven species of *Aristea* known anatomically lack this tissue (Rudall, 1995; J. Manning, pers. comm.), instead having columnar epidermal cells with thickened anticlinal walls. Both anatomical conditions are probably universal for the genus but are scored only for the species in which they are known. Septal nectaries are considered to be the plesiomorphic condition in Nivenioideae (Goldblatt, 1993). They occur in *Patersonia* (P. Rudall, pers. comm.) and in *Nivenia*, *Klattia*, and *Witsenia* (Goldblatt, 1993). Flowers of nearly all species of *Aristea* lack nectar (unpublished observations), but *A. spiralis* does secrete nectar, which has been found to be produced from perigonal nectaries located near the tepal bases (J. Manning, pers. comm.), an autapomorphy for that species. The above three characters contain no information relevant to the relationships of members of the ingroup but seem unambiguously to establish the monophyly of *Aristea*, which has few apomorphic morphological features. The only apparent specialized feature in *Aristea* is the vestigial perianth tube. Papillate outer epidermal cells of the seed coat, present in the few species examined for the character, may be another. No other genus of Iridaceae is known to have such epidermal cells in the seed coat (unpublished data).

Characters of the species of *Aristea* examined here were combined with data for several more for which there is palynological information (Goldblatt & Le Thomas, 1992a), assembled in a matrix (Table 2), and analyzed using the Hennig86 package of programs for phylogenetic analysis (Farris, 1988). The data set, including 33 characters and up to 36 taxa, took considerable time to run using the ie option (generating trees by implicit enumeration). We thus decided to use the mh* bb* options for the analysis, which applies branch swapping to each of the initial trees and saves all the shortest trees generated. Tree lengths, and consistency and

Table 2. Data matrix and character list for *Aristea*. Multistate characters are 1, 4, 9, 11, 12, 13, 14, 15, 18, 19, 20, 24, and 33; of these 4, 9, 12, 14, and 18 are additive or arbitrarily divided grades in a more or less continuous range of variation and are treated as ordered states. Characters are scored ? if unknown or intermediate between two states [Note: some scorings change for the matrix that includes Ixioideae, and an additional character, 34, is added for this analysis.]

1. Pollen grain apertures restricted to one surface, usually monosulcate, rarely trichotomosulcate (0)—grains sulculate (1); 2-zonasulculate (2); grains 3-sulcate or spiraperturate (3)
2. Aperture membrane smooth to granular, without exine fragments (0)—aperture membrane with exine fragments, sometimes forming an operculum-like median band (1)
3. Aperture border not diffuse (0)—aperture border diffuse (1)
4. Exine lumina large (0)—medium-sized (1); small (2)
5. Exine surface (muri or areolae) smooth (0)—exine surface sculpted (1)
6. Exine surface without perforations (0)—surface with perforations (1)
7. Pollen grains smaller (diameter less than 65 μm) (0)—larger (diameter more than 70 μm) (1)
8. Pollen always shed in monads (0)—pollen often shed in tetrads (1)
9. Exine reticulate (0)—rugulate (1); rugulo-areolate (2)
10. Rhipidial spathes prominent, enclosing the entire inflorescence (0)—spathes not prominent and buds and floral bracts evident (1)
11. Capsules round to lightly 3-lobed in section (0)—capsules 3-winged (1); capsules 3-lobed (2); deeply divided into 3 lobes, each widest in the middle (3)
12. Capsules in profile more or less ovoid (0)—capsules oblong (1); capsules elongate (2)
13. Capsule walls brittle and dehiscing normally (0)—walls thin, dehiscing on the septa (1); walls thick and woody, tardily dehiscent (2)
14. Seeds numerous to several per locule (0)—seeds usually 4 per locule (1); seeds 2 per locule (2)
15. Seeds rounded to prismatic (0)—seeds radially compressed (1); seeds nearly cylindric and obliquely truncate at both ends (2); seeds globose with an aril (3)
16. Anthers ovoid-oblong (0)—anthers narrrow and linear (1)
17. Anthers longitudinally dehiscent (0)—anthers apically dehiscent (porose) (1)
18. Lateral rhipidia all terminal on branches, thus stalked (0)—some lateral rhipidia sessile (1); all lateral rhipidia normally sessile (2)
19. Compound inflorescence racemose, spicate, or subpaniculate (0)—subdichotomously branched (1); 1–2 subterminal flower clusters (2)
20. Stem lightly compressed to terete in upper half (0)—stem strongly compressed and broadly winged throughout (1); narrow and ancipitous (2)
21. Outer tepal whorl similar to inner (0)—outer and inner whorls differentiated in size and color (1)
22. Flowers more or less upright (0)—flowers secund (1)
23. Style lobed apically and the lobes fringed (0)—style minutely notched apically (1)
24. Rhipidial spathes and floral bracts green to brownish and chartaceous (0)—spathes and bracts silvery and scarious with entire margins (1); with regularly fringed, rust-colored margins (2)
25. Septal nectaries present (0)—septal nectaries absent (1)
26. Flowering stem bearing a few leaves decreasing in size above (0)—basal internode very long, leafless except for a subterminal bract-like leaf (1)
27. Flowering stems exceeding the leaves and plants not cushion-like tufts (0)—flowering stems short and plants low cushion-like tufts (1)
28. Inflorescences with several to few flower clusters (0)—compound inflorescence massively enriched (1)
29. Seed surface with primary sculpturing, usually rugose (0)—surface without primary sculpturing (1)
30. Leaf margins with subepidermal sclerenchyma (0)—without subepidermal sclerenchyma (1)
31. Perianth tube well developed (0)—vestigial (1)
32. Outer tepals symmetric about the midvein (0)—asymmetric (2)
33. Tepals uniformly deep blue (0)—tepals pale blue to whitish (1); tepals shades of mauve to turquoise (or cream) (2)
Additional character when Ixioideae is added to matrix
34. Flowers lasting at least one day and not deliquescing on fading (0)—flowers fugaceous, lasting less than a day and deliquescing on fading (1) [scored 0 for *Nivenia* and Ixioideae, 1 for all species of *Aristea*]
[Autapomorphies not included: exine with supratectal verrucae (*A. spiralis*); perigonal nectaries (*A. spiralis*); flower clusters pendent (*A. singularis*); spathes and bracts regularly fringed (*A. africana*); spathes and bracts lacerate (*A. woodi*).]

Table 2.   Continued.

Taxon	12345	1 67890	11111 12345	11112 67890	22222 12345	22223 67890	333 123
				Character Number			
Nivpat	00010	00000	000?0	000?0	00000	00000	000
africana	30001	11001	10121	00010	00021	01001	100
anceps	11121	10010	01000	00221	00001	1000?	100
teretifolia	20000	11000	32202	10200	10001	0000?	112
biflora	20000	10000	32202	10200	10001	01001	112
cantharophila	20101	10000	32202	10200	00001	0000?	102
monticola	00020	00011	10011	00100	00101	00101	100
juncifolia	00010	00001	11011	00200	00101	0001?	100
fimbriata	00010	?1001	11??1	00100	00121	010??	100
confusa	00020	00001	11011	00100	00101	0011?	100
dichotoma	30001	11001	10121	00012	00011	0100?	100
ecklonii	11111	10111	21000	00101	00001	00001	100
glauca	30000	11001	10121	00012	00011	0100?	100
lugens	20000	11000	32202	10200	10001	0000?	101
major	00020	00001	10021	00100	01101	0011?	100
spiralis	21120	01000	32202	10201	01001	00001	101
simplex	21111	11000	32202	10200	01001	0000?	101
schizolaena	00120	00001	00000	00200	00001	0000?	100
goetzei	11120	10021	00000	00201	00001	0000?	100
humbertii	11120	100?1	00000	01110	00001	0010?	100
cladocarpa	11121	10011	21000	00101	00001	0000?	100
madagascariensis	11120	10021	00000	01200	00001	0000?	100
kitchingii	11120	10021	00000	01100	00001	0010?	100
angustifolia	11120	10011	00000	00200	00001	0000?	100
nyikensis	11120	10021	00000	00100	00011	0000?	100
ranomafana	11120	10021	00000	01010	00001	0010?	100
polycephala	11120	10021	00000	00010	00011	0000?	100
racemosa	00010	00001	11011	00200	00101	001??	100
pusilla	11121	10110	21000	00101	00001	0000?	100
angolensis	11111	10011	00000	00100	00011	00001	100
oligocephala	30001	11001	10121	00010	00011	0000?	100
platycephala	1112?	10011	20020	00201	00001	0000?	100
abyssinica	11111	10011	00000	00121	00001	1000?	100
singularis	00020	00011	10123	00010	00001	0100?	100
pauciflora	20001	11000	32202	00200	00001	00001	100
woodii	11111	10011	00000	00200	00001	0000?	100
montana	11111	10001	00000	00100	00001	0000?	100
grandis	11120	?0011	00000	00200	00001	0000?	100

retention indices (Figs. 47, 49), are automatically calculated by Hennig86 (Farris, 1988). Because the initial trees were poorly resolved, the successive weighting option was also invoked. Successive weighting, recommended by Farris (1969) for situations where unreliable (homoplasious) characters outnumber reliable ones, is one way to improve tree resolution. The method selectively weights those characters that are more consistent at the expense of those that are homoplasious. The method may be extremely helpful especially when more conventional analyses yield large numbers of trees and consensus trees are poorly resolved. Cladograms were then analyzed using CLADOS (Nixon, 1992) and the trees presented here were generated using this program. We were unable to determine a measure of confidence in the trees obtained by successive weighting by bootstrap analysis (Swofford, 1991) because the number of trees generated using the method was so large in some replicates that it became impractical to perform.

A second series of cladistic analyses was performed after the addition of one more taxon, subfamily Ixioideae, to the matrix. This was because in recent molecular systematic studies using sequences from two chloroplast genes, rbcL and rps4

(M. Chase et al., 1995, and pers. comm.; Souza-Chies et al., 1997), the subfamily has been found to be nested in Nivenioideae, as a sister clade either to *Nivenia* plus *Witsenia* or *Aristea*. Consequently, we were interested to see how this might affect the topology of the trees.

RESULTS

PALYNOLOGY

Shape and Size. In hydrated or rehydrated pollen, grains are ellipsoid to nearly spherical. Pollen is typically shed in monads, but in *Aristea ecklonii* and *A. pusilla* the tetrad stage is evidently prolonged, and most pollen is shed as tetrads, a specialized condition (Figs. 1, 2).

Species of *Aristea* fall fairly well into two size classes for pollen-grain size (Table 1). Nineteen of the species examined have medium-sized to moderately large grains (equatorial diameter 45–64 μm) and 13 species have large grains (equatorial diameter more than 69–97.5 μm). *Aristea schizolaena*, with grains 66.7 × 60.0 μm, falls between the two groups. Pollen-grain size among the species examined ranges from a minimum of 45.5 × 42.0 μm in *A. major*, to a maximum of 97.5 × 85.5 μm in *A. oligocephala*, and 97.5 × 93.0 μm in *A. dichotoma*. Species of the outgroup have grains that fall in the medium to moderately large size category (Manning & Goldblatt, 1989), hence this is presumed to be the plesiomorphic condition. Size is correlated with some aspects of Weimarck's (1940) infrageneric classification (Table 1). The four species of section *Aristea* examined all have grains exceeding 80 × 77 μm. The remaining species of that section, *A. recisa*, has grains of comparable size according to measurements given by Schulze (1971a). Only *A. lugens* and *A. teretifolia* (sect. *Pseudaristea*) have comparably large grains. Most other species of section *Pseudaristea* (as redefined by Goldblatt, 1995a) have somewhat smaller grains, more than 71 × 70 μm, and are thus still classified as large according to our definition. Grains of species of section *Racemosae*, excepting *A. fimbriata*, are medium-sized, as are those of sections *Eucapsulares*, *Trilobatae*, *Cladocarpa*, and *Ancipites* (Table 1), including those of the Madagascan species (Goldblatt & Le Thomas, 1992a). Except for *A. schizolaena*, grains of members of these sections have an equatorial diameter less than 65 μm. Pollen grains of the outgroup are less than 65 μm in diameter, hence medium-sized grains are scored 0 and large grains as 1. *Aristea schizolaena*, which has grains intermediate in size between the two size classes, is scored as ?.

Apertures. Pollen-grain apertures are remarkably variable for a genus the size of *Aristea*. In many cases, correct terminology (sensu Punt et al., 1994) cannot be established because we lack developmental stages necessary for its definition. In our analysis, we recognize four main apertural types. These are treated as four unordered states of one character. The aperture types are as follows.

1. The monosulcate type, which is the plesiomorphic condition for the family based on outgroup comparison (e.g., Goldblatt, 1990). Apertures have been observed in some species at the tetrad stage and determined to be distal, and can reasonably be assumed to be so whenever apertures are unambiguously sulcate (Figs. 3–6, 10, 11). We include in this category the trichotomosulcate aperture of *A. fimbriata* (Fig. 37) because, although the aperture in the species is recognizably different from truly monosulcate apertures, it seems to us to belong in the same general class, being restricted to one face of the pollen grain.

Monosulcate grains are present in five of six species of section *Racemosae* examined (*Aristea confusa, A. juncifolia, A. major, A. monticola, A. racemosa*) and in *A. schizolaena* and *A. singularis*. Among the species examined by Schulze (1971a), *A. macrocarpa* (sect. *Racemosae*) also has monosulcate pollen grains. *Aristea fimbriata*, also section *Racemosae*, alone has trichotomosulculate grains (Fig. 38). As in grains with monosulcate apertures, the aperture is generally wide, reaching the ends of the grain and sometimes extending a short distance onto the non-apertural face. The aperture membrane is typically smooth, that is without substantial amounts of exine on the surface, and the margins are clearly defined. Occasionally tiny fragments of exine are present, visible only using LM (e.g., in *A. fimbriata*).

2. The sulculate type, which includes 1-zonasulculate and disulculate grains, the distinction, in some cases, being difficult to establish because they may occur together in the same species, even in the same sample, and there are often forms intermediate between the two, for example, in species like *A. kitchingii* (Goldblatt & Le Thomas, 1992a) (Figs. 13–24).

Sulculate grains are the most common type in the genus and are found in 19 species of tropical and eastern southern Africa as well as in 6 of the 7 species that occur in Madagascar. In these grains the aperture is typically obscure and the apertural membrane is covered by more or less disorganized exine, sometimes consisting of an almost complete band, free or not at the ends of the apertures (thus an operculum or pontoperculum) especially in spe-
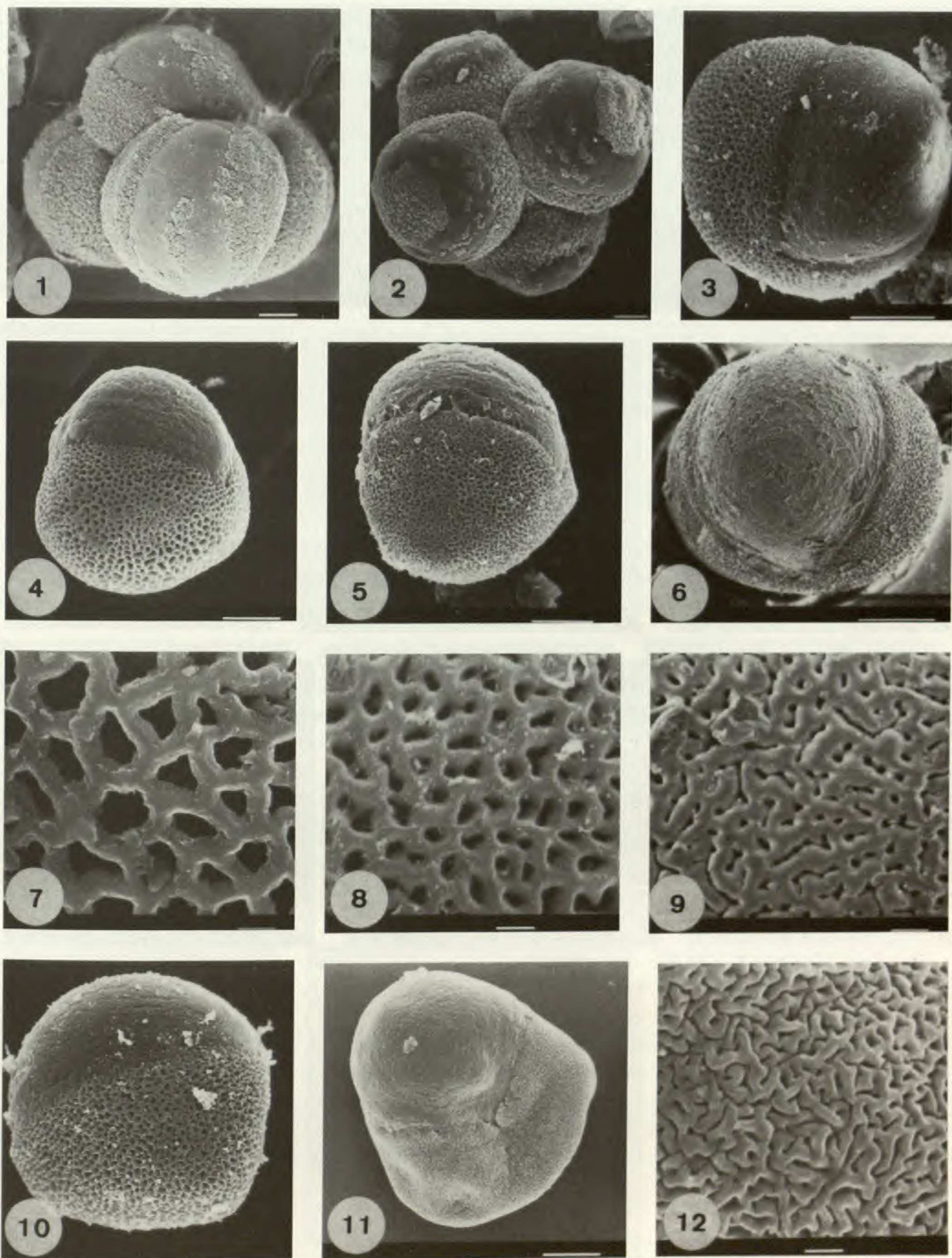
Figures 1–12. —1. *Aristea ecklonii*: mature grains in tetrads.—2. *Aristea pusilla*: tetrads of mature pollen. 3–12. Monosulcate pollen grains of sections *Racemosae*, *Singularis*, and *Eucapsulares* with exine detail for selected species.—3. *A. major.*—4 & 7. *A. juncifolia.*—5 & 8. *A. confusa.*—6 & 9. *A. monticola.*—10. *A. schizolaena* (sect. *Eucapsulares*).—11, 12. *Aristea singularis* (sect. *Singularis*). Scale bar: whole grains 10 μm; sculpturing detail 1 μm.

cies (Goldblatt & Le Thomas, 1992a) of Madagascar. The aperture margins are usually diffuse and the ends of the apertures are often difficult to see, apparently sometimes extending around the entire grain (as a zonasulculus—Figs. 13, 15, 19) or interrupted by exine (then evidently disulculate—Fig. 24).

3. The 2-zonasulculate type (Le Thomas &
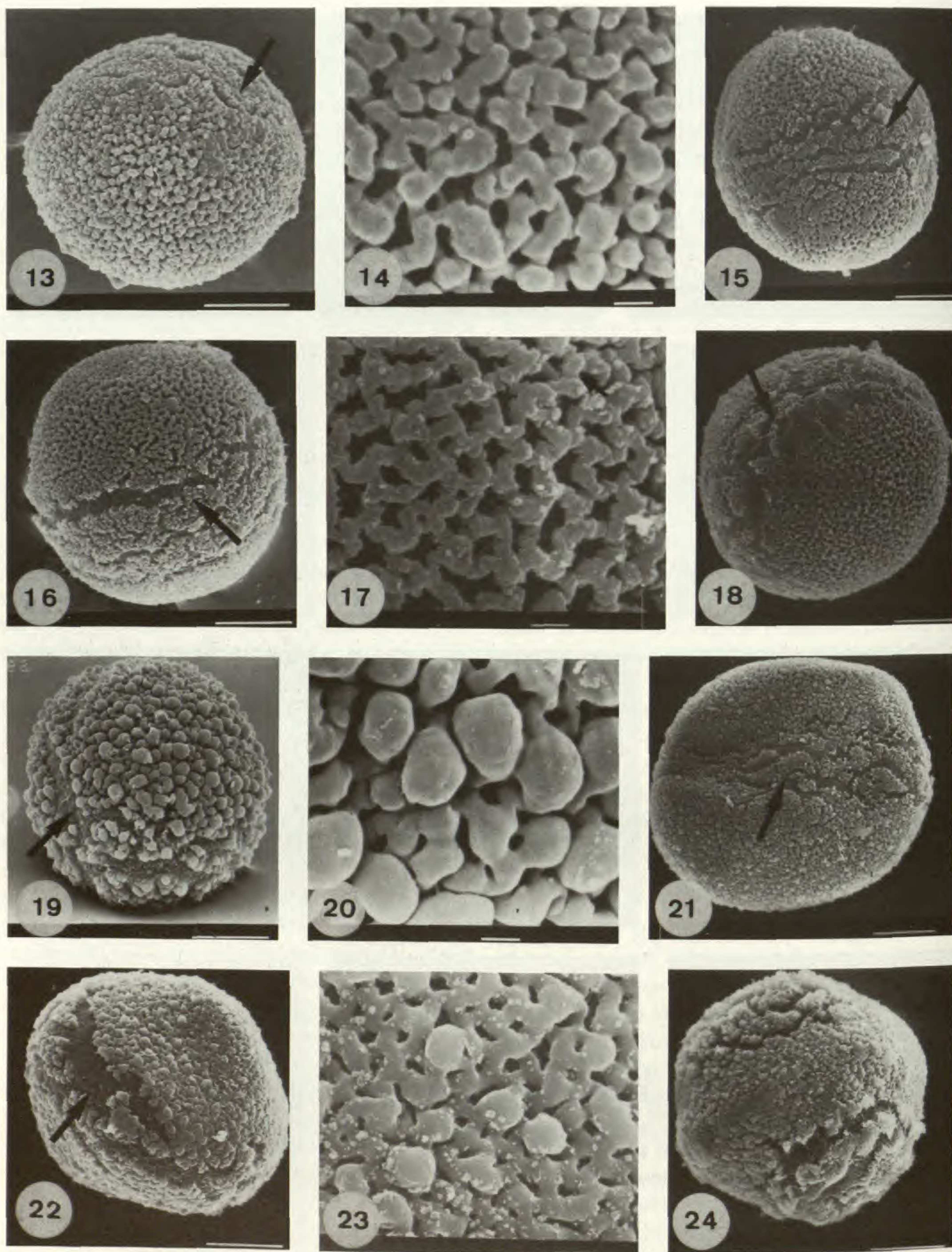
Figures 13–24. Sulculate pollen grains of section *Eucapsulares* with exine sculpturing in selected species.—13, 14. *Aristea grandis.*—15. *A. angolensis.*—16, 17. *A. montana.*—18. *A. abyssinica.*—19, 20. *A. goetzei.*—21. *A. nyikensis.*—22, 23. *A. ranomafana.*—24. *A. polycephala.* Arrows indicate the apertural zone when not obvious. Scale bar: whole grains 10 μm; sculpturing detail 1 μm.

Goldblatt, 1994; Le Thomas et al., 1996) in which there are two clearly defined zonasulculi (Figs. 25–34), an extremely rare type of pollen grain in flowering plants.

Two-zonasulculate apertures occur in all seven species of section *Pseudaristea* (Table 1). Here, the margins are usually clearly defined (Figs. 26, 29, 31, 34), but in *A. spiralis* (Fig. 35) and *A. pauciflora*
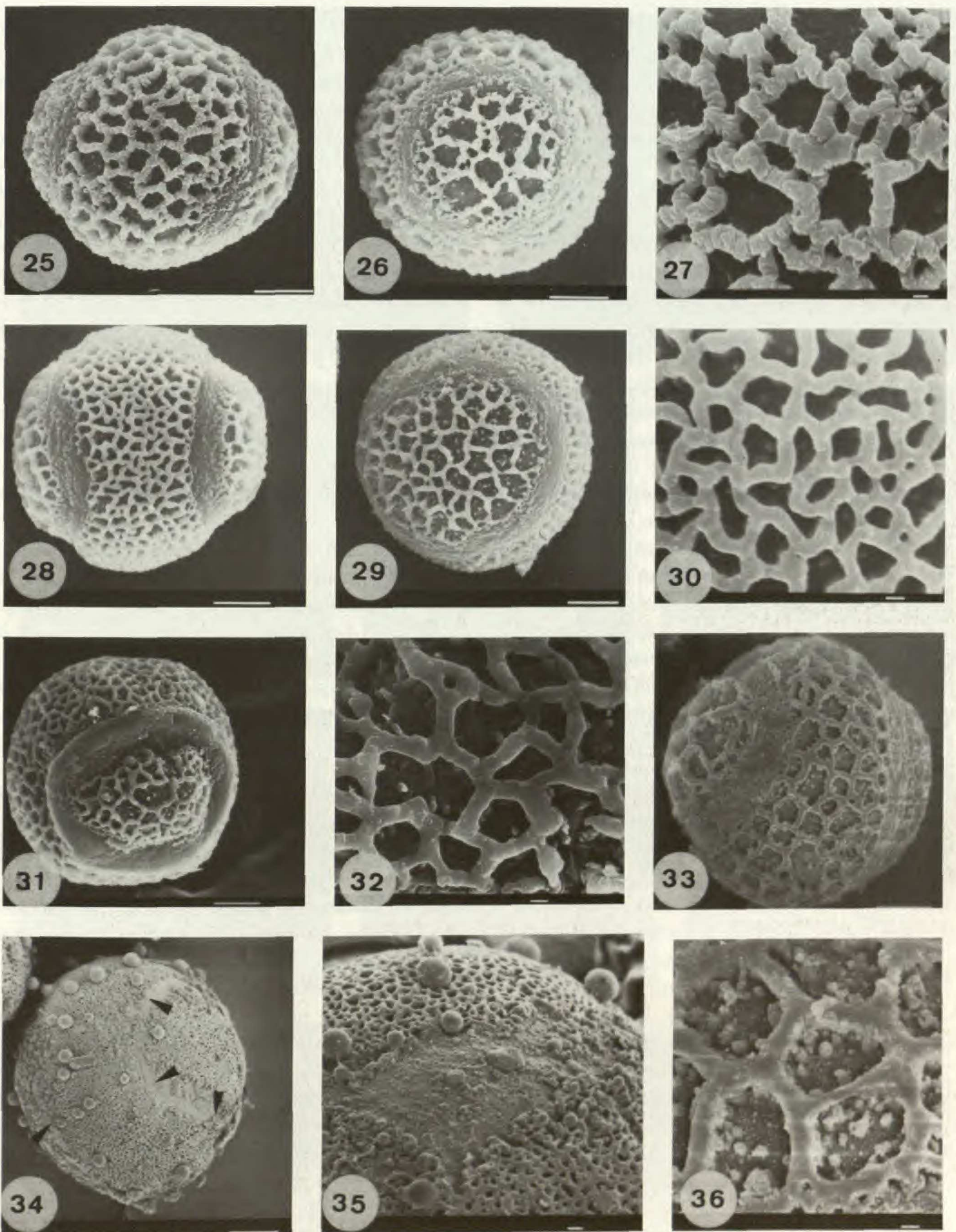
Figures 25–36.   Two-zonasulculate pollen grains of section *Pseudaristea* as redefined here, with exine and aperture detail for selected species.—25–27. *Aristea cantharophila*, equatorial and polar view of grains.—28–30. *A. biflora*, equatorial and polar view of grains.—31, 32. *A. lugens.*—33 & 36. *A. teretifolia.*—34, 35. *A. spiralis*, whole grain with arrows pointing to the two zonasulculi, and aperture detail showing diffuse margins, apertural exine fragments, and supratectal exine gemmules. Scale bar: whole grains and apertural detail of *A. spiralis* 10 μm; sculpturing detail 1 μm.

(Le Thomas et al., 1996) they are somewhat diffuse and the apertural membrane is covered with small, scattered fragments of exine. This aperture type is usually constant within a species, but in our sample of *A. simplex*, 2-zonasulculate grains occurred together with some 1-zonasulculate grains. The 1-zonasulculate condition may represent the intermediate phase in the evolution of the 2-zonasul-

culate grain. Pollen of an unidentified plant, apparently closely allied to *A. pauciflora*, but lacking both well-preserved flowers and mature capsules and seeds, has exclusively 1-zonasulculate grains with clearly defined margins and without diffuse exine fragments on the apertural membrane (Fig. 45). These grains recall the 1-zonasulculate grains found in our sample of *A. simplex*. The plant also bears a fair resemblance to *A. zeyheri*, but specimens identified with this species (Weimarck, 1940) clearly belong to section *Racemosae*, close to *A. racemosa*. Like it, they have monosulcate grains (three collections checked under the light microscope). Because of the uncertain identity of the species with these 1-zonasulculate grains, and because so many of its morphological characters are unknown, we were unable to include it in the phylogenetic analysis. This plant, evidently representing an undescribed species, should be investigated in more detail when opportunity arises.

4. The 3-sulcate (or more or less spiraperturate) type (Le Thomas & Goldblatt, 1994; Le Thomas et al., 1996, Goldblatt et al., 1997), known elsewhere in Iridaceae, with well-defined apertural zones separating equal or unequal plates of exine and the sulci always confluent (Figs. 39–41).

Three-sulcate grains are restricted to three of the four species of section *Aristea* examined, and a fifth, *A. recisa*, examined by Schulze (1971a), probably also has this aperture type although it was not specifically so described by him. In *A. oligocephala* of the section, the apertures are difficult to define and are more or less spiraperturate, consisting of several confluent sulci separated by large plates of exine of varying size. The tendency for the spiralization of the aperture apparently corresponds to Schulze's (1971a) observations for the species based on examination of acetolyzed pollen.

In addition to the aperture itself, two more apertural characters are recognized, the nature of the margin and the apertural membrane. Margins are either sharply defined (e.g., Figs. 3–6), the plesiomorphic condition based on outgroup comparison (Manning & Goldblatt, 1989), or diffuse (e.g., Fig. 35). The ancestral condition, again based on outgroup comparison (Goldblatt & Manning, 1989), for the aperture membrane is without fragments of exine (i.e., smooth) (e.g., Figs. 3–5, 39, 40), and in the derived state the membrane is more or less obscured by irregularly shaped, fairly large fragments of exine (e.g., Figs. 13, 15, 16, 21) that sometimes form an operculum-like band (Goldblatt & Le Thomas, 1992a).

Surface sculpturing. The exine is tectate-colu-

mellate and the exine patterning ranges from reticulate (Fig. 7, 8, 42–44), to rugulate (Fig. 9, 12), and rugulo-areolate (Fig. 20, 23), depending on the size and shape of the lumina and the orientation of the muri with respect to one another as well as their overall shape. The character states form a continuum and the distinction between them, although clearly defined by terminology (Punt et al., 1994), is arbitrary. The states thus constitute an ordered series of one character. Lumen size is regarded as a separate character from basic exine pattern, and outgroup comparison suggests that lumina of moderate size (1–2 μm in diameter), as for example, in *Aristea confusa* and *A. montana* (Figs. 7, 17), are the plesiomorphic condition for the genus. A reticulum with large lumina (2–6 μm in diameter) characterizes *A. africana*, *A. glauca*, and *A. cantharophila* (e.g., Figs. 27, 42–44), and in these species the bases of the lumina are often prominently verrucate or baculate. Small lumina (less than 1 μm, i.e., microreticulate) characterize *A. juncifolia*, *A. angolensis*, and *A. spiralis*, among others (e.g., Figs. 8, 15, 35). Lumina are normally fairly similar in size, all or most falling in the same size class for a particular sample. *Aristea cantharophila* is, however, exceptional in having mostly large lumina mixed with small lumina on the distal exine plates (Fig. 26). The three states of lumen size are arbitrary divisions of a continuum and intrinsically additive, and the character is treated as ordered.

The exine muri are variable in shape and sculpturing, most often angular and smooth, especially when the lumina of the reticulum are of moderate or small size, but more or less wavy, sculpted, and with perforations when the lumina are large. The species of section *Africana* and some of section *Pseudaristea* are notable for their ridged exine muri (Figs. 27, 42, 44). A remarkable feature of the exine of *A. spiralis* is the presence of large, irregularly distributed, supratectal gemmules on the reticulum (Figs. 34, 35), a condition reported for this species by Radelescu (1970). This recalls the exine of one species of the outgroup, *Witsenia maura* (L.) Thunb., which is autapomorphic in having large verrucae lying on a more or less microreticulate tectum (Manning & Goldblatt, 1989). A typical rugulate sculpturing with more or less elongate exine elements, free or incompletely fused, occurs in *A. monticola* and *A. singularis* (Figs. 9, 12), but in some species in this category the rugulae are contorted, very irregular in shape, and more or less fused (e.g., *A. grandis*—Fig. 14). In this type, the surface of the muri may be smooth or sculpted. All the Madagascan endemic species (Table 3), plus *A. goetzei* and the tropical African endemic *A. nyiken-*
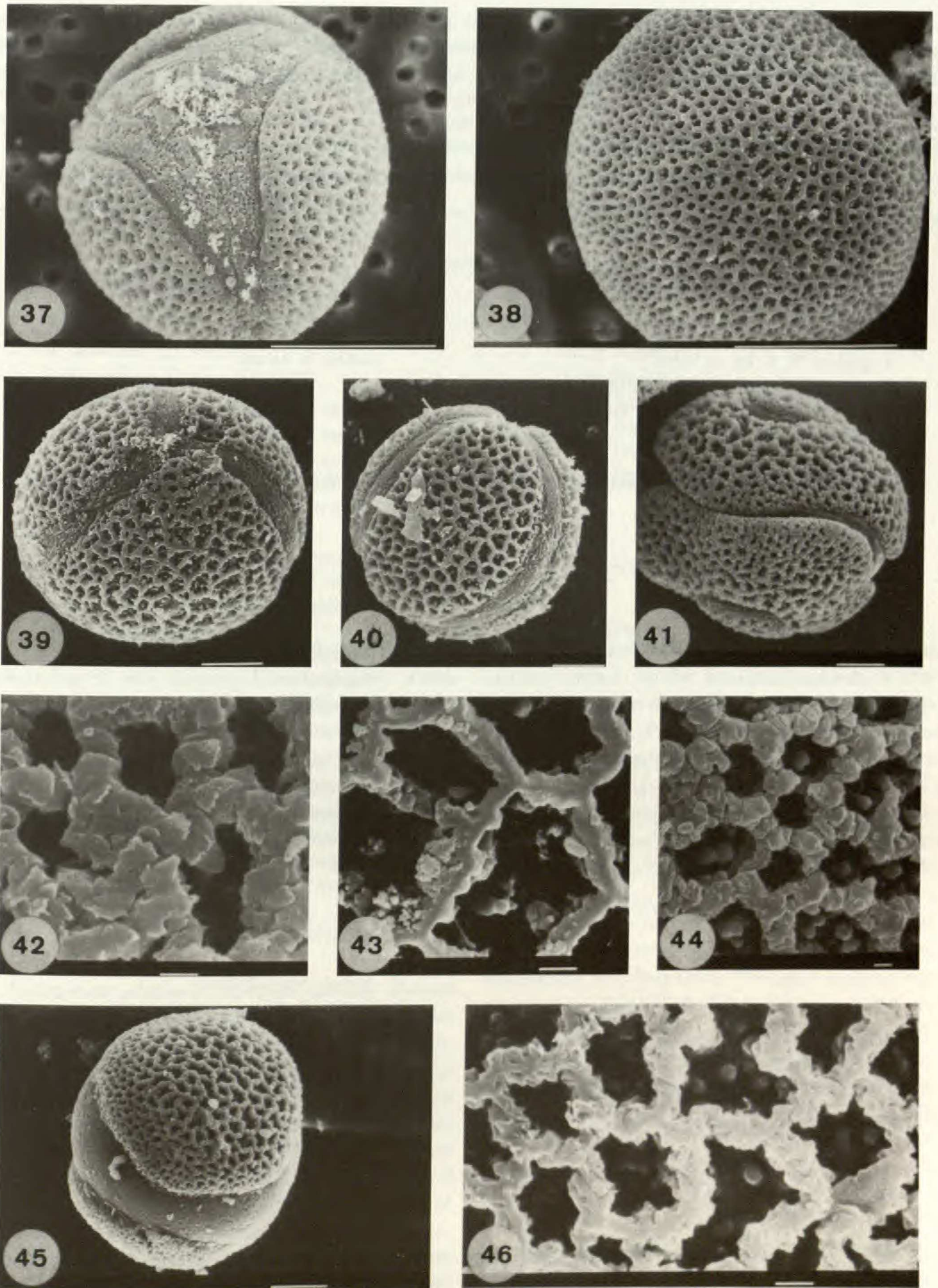
Figures 37–46. 37, 38. Pollen grains of *Aristea fimbriata* (sect. *Racemosae*), section *Aristea* and *A. sp.* (aff. *A. pauciflora*) with exine detail for selected species.—37, 38. *A. fimbriata*, showing apertural and non-apertural surfaces of grains.—39 & 42. *A. africana.*—40 & 43. *A. glauca.*—41 & 44. *A. oligocephala.*—45, 46. *A. sp.* (aff. *pauciflora*). Scale bar: whole grains 10 μm; sculpturing detail 1 μm.

Table 3. Species of *Aristea* with their geographic ranges arranged according to the revised classification proposed here. There are 50 species currently recognized in the genus, one or possibly two undescribed species in section *Racemosae*, and the plant referred to in the text as *G.* sp. *aff. pauciflora* may be an undescribed species of section *Pseudaristea*. Species marked with * are unknown palynologically; those with @ are at least known for the aperture but were not included in the phylogenetic analysis because other pollen characters are unknown. Figures in parentheses are total species in the taxon. The type species of the subgenera and sections are indicated in bold type.

Taxon	Geographical range
Subgenus *Eucapsulares* Goldblatt (24)	
The *A. angolensis* group (= sect. *Aristea* sensu Weimarck) (12)	
A. angolensis Baker (incl. *A. flexicaulis* Baker)	Cameroon and Ethiopia to eastern S. Africa
A. angustifolia Baker	Madagascar
A. compressa Buch. ex Baker*	eastern S. Africa
A. galpinii N. E. Br. ex Weim.*	eastern S. Africa
A. gerrardii Weim.* (closely related to	
A. compressa and possibly not distinct)	eastern S. Africa
A. grandis Weim.	eastern S. Africa
A. montana Baker	eastern S. Africa
A. goetzei Baker (= *A. nitida* Weim.)	Tanzania and Madagascar
A. nyikensis Baker (incl.	southern tropical Africa
A. hockii de Wild)	
A. polycephala Harms	southern tropical Africa
A. schizolaena Harv. ex Baker	eastern S. Africa
A. woodii N. E. Br.	southern tropical and eastern S. Africa
The *A. madagascariensis* group (4)	
A. humbertii H. Perr.	Madagascar
A. kitchingii Baker	Madagascar
A. madagascariensis Baker	Madagascar
A. ranomafana Goldblatt	Madagascar
The *A. ecklonii* group (incl. section *Trilobatae* Weim. and section *Cladocarpae* Weim.) (5)	
A. cladocarpa Baker	Madagascar
A. ecklonii Baker	Cameroon and Uganda to eastern S. Africa
A. ensifolia Muir*	southern Cape Region
A. platycephala Baker	eastern S. Africa
A. pusilla (Thunb.) Ker Gawl.	eastern S. Africa and Cape Region
The *A. anceps* group (= section *Ancipites* Weim.) (3)	
A. abyssinica Pax (incl.	Ethiopia to eastern S. Africa
A. cognata N. E. Br.)	
A. alata Baker*	eastern tropical Africa
A. anceps Ecklon	eastern S. Africa
Subgenus *Pseudaristea* Pax (7)	
A. biflora Weim.	Cape Region
A. cantharophila Goldblatt	
& J. Manning	Cape Region
A. lugens (L.f.) Weim.	Cape Region
A. pauciflora W. Dod.	Cape Region
A. spiralis (L.f.) Ker Gawl.	Cape Region
A. simplex Weim.	Cape Region
A. teretifolia Goldblatt & J. Manning	Cape Region
Subgenus *Aristea* (21)	
Section *Racemosae* Weim. (13)	
A. bakeri Klatt* (doubtfully distinct from *A. confusa*)	Cape Region
A. confusa Goldblatt	Cape Region
A. cuspidata Schinz*	Cape Region
A. fimbriata Goldblatt & J. Manning	Cape Region
A. inaequalis Goldblatt & J. Manning@	Cape Region
A. juncifolia Baker	Cape Region
A. macrocarpa G. Lewis@	Cape Region

Table 3. Continued.

Taxon	Geographical range
A. major Andrews	Cape Region
A. monticola Goldblatt	Cape Region
A. racemosa Baker	Cape Region
A. rigidifolia G. Lewis*	Cape Region
A. rupicola Goldblatt & J. Manning@	Cape Region
A. zeyheri Baker@	Cape Region
Section *Singulares* Weim. (1)	
A. singularis Weim.	Cape Region
Section *Aristea* (6)	
A. africana (L.) Hoffmsg.	Cape Region
A. dichotoma (Thunb.) Ker Gawl.	Cape Region
A. glauca Klatt	Cape Region
A. oligocephala Baker	Cape Region
A. palustris Schltr.*	Cape Region
A. recisa Klatt@ (closely allied to and perhaps not distinct from *A. africana*)	Cape Region
Uncertain position (Lewis, 1952)	
A. latifolia G. Lewis*	Cape Region

sis (Figs. 20, 21), have a rugulo-areolate sculpturing consisting of very closely aligned rugulae, which sometimes conform to the strict definition of areolae.

In addition to the basic exine patterning we recognize two additional exine characters: surface smooth or sculpted, and with or without perforations. Outgroup comparison indicates that both the smooth condition and the absence of perforations are ancestral.

PHYLOGENY

Preliminary cladistic analyses quickly showed that the data are homoplasious for many characters and that numerous (usually over 1000) trees were obtained whatever option was chosen from the Henning86 package for the analysis. The resulting consensus trees, however poorly resolved, always embodied a number of distinct clades (Fig. 47A). Most notable among them are the clades at nodes 1 and 2 of Figure 47A. Node 1 includes those species of Weimarck's section *Pseudaristea* that have 2-zonasulculate pollen grains combined with elongate capsules, locules deeply lobed longitudinally, and truncated seeds. Node 2 includes Weimarck's sections *Aristea* and *Racemosae* (capsules with prominent narrow wings, radially flattened seeds, and a reduced seed number per locule), plus *A. singularis* (sect. *Singularis*), which has rounded seeds with an aril but winged capsules.

Successive weighting yielded a dramatic reduc-

tion in the number of trees and a rise in the consistency index. In the final analysis we obtained just 24 trees that differed minimally, and the strict consensus tree (Fig. 47B) is relatively well resolved. Most significantly, what we call the core species of section *Pseudaristea* (clade 1), also a clade in the unweighted consensus tree, formed a sister clade to the remaining species of the genus (clade 2). The first bifurcation of clade 2 divides its constituent species fairly evenly. Clade 3 of Figure 47B corresponds exactly to clade 2 of the unweighted consensus tree, that is, sections *Aristea*, *Racemosae*, and *Singularis*. The three sections each constitute a single clade (Fig. 47B, clades 5, 6, and 7). The division corresponds closely to Weimarck's (1940) sectional composition. Clade 3 is supported by fruit and seed characters (winged capsules, radially flattened seeds, few seeds per locule) (Fig. 48).

The poorly resolved sister clade at node 4 includes species of five of Weimarck's sections: all the members of his sections *Eucapsulares* (which he called *Euaristea*) and *Ancipites*; the monotypic sections *Trilobatae* (*A. platycephala*) and *Cladocarpae* (*A. cladocarpa*); and two species of his section *Pseudaristea*, *A. ecklonii* and *A. pusilla*. There is little support for any large species clusters in clade 4. Notable smaller clades include those at nodes 8, 9, and 10. Clade 8 includes two species of Weimarck's section *Pseudaristea*, plus the single species each of his sections *Cladocarpae* and *Triloba-*
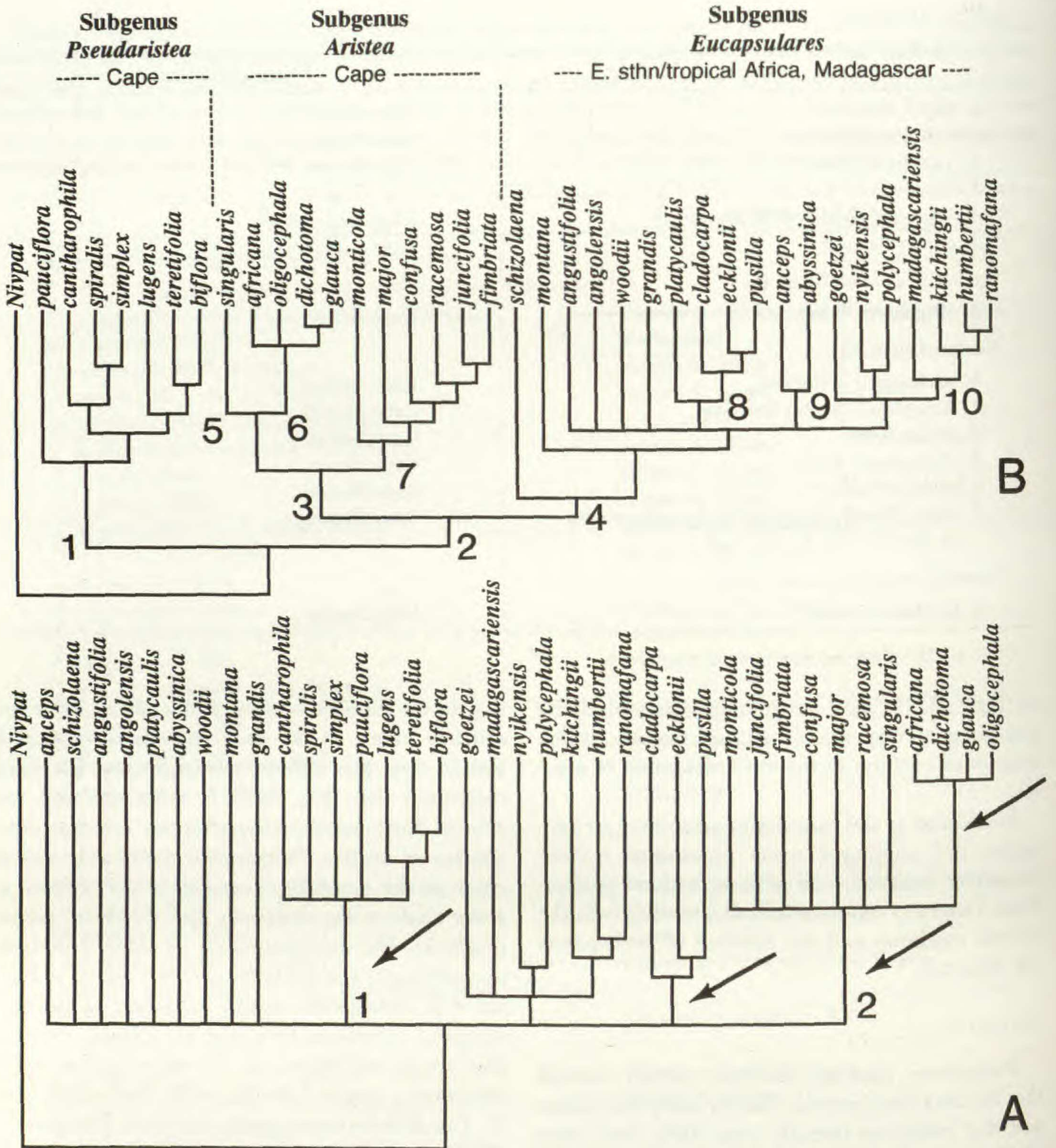
Figure 47. Cladograms showing species relationships in *Aristea* using the matrix in Table 2 with the outgroup *Nivpat.*—A. Strict consensus tree of 1012 equally parsimonious trees obtained using the mh* and bb* options of Hennig86, length (L) 107, consistency index (CI) 45, retention index (RI) 80. Arrows show clades present in all analyses. Clade 1 corresponds to the core species of Weimarck's section *Pseudaristea* and 2, to sections *Aristea, Racemosae,* and *Singularis.*—B. Strict consensus tree of 24 equally parsimonious trees (CI 76, RI 93) obtained using the mh* and bb* options of Hennig86 followed by successive weighting (xs w). The three subgenera of the revised classification proposed as a result of the analysis are shown above the main clades. Geographical distribution of the subgenera is also indicated.

tae. Clade 9 includes the two species of section *Ancipites* included in our analysis, and clade 10 has the four Madagascan species with porose anther dehiscence. In the tree selected for plotting characters (Fig. 48), clades 8 and 9 are united (compare with the strict consensus tree, Fig. 47B). The isolated position of *Aristea schizolaena* in clade 4 (Fig. 47B) is difficult to explain in terms of morphology and

is discussed below. The topology of the weighted consensus tree produced using the matrix that included the extra taxon, Ixioideae, differs only slightly. In this tree (Fig. 49) Ixioideae falls outside *Aristea* and the three main clades (nodes 1, 2, and 4) are the same as in the analyses without Ixioideae (compare with Fig. 47B). The position of clades 1 and 2 with respect to clade 3 is, however, reversed
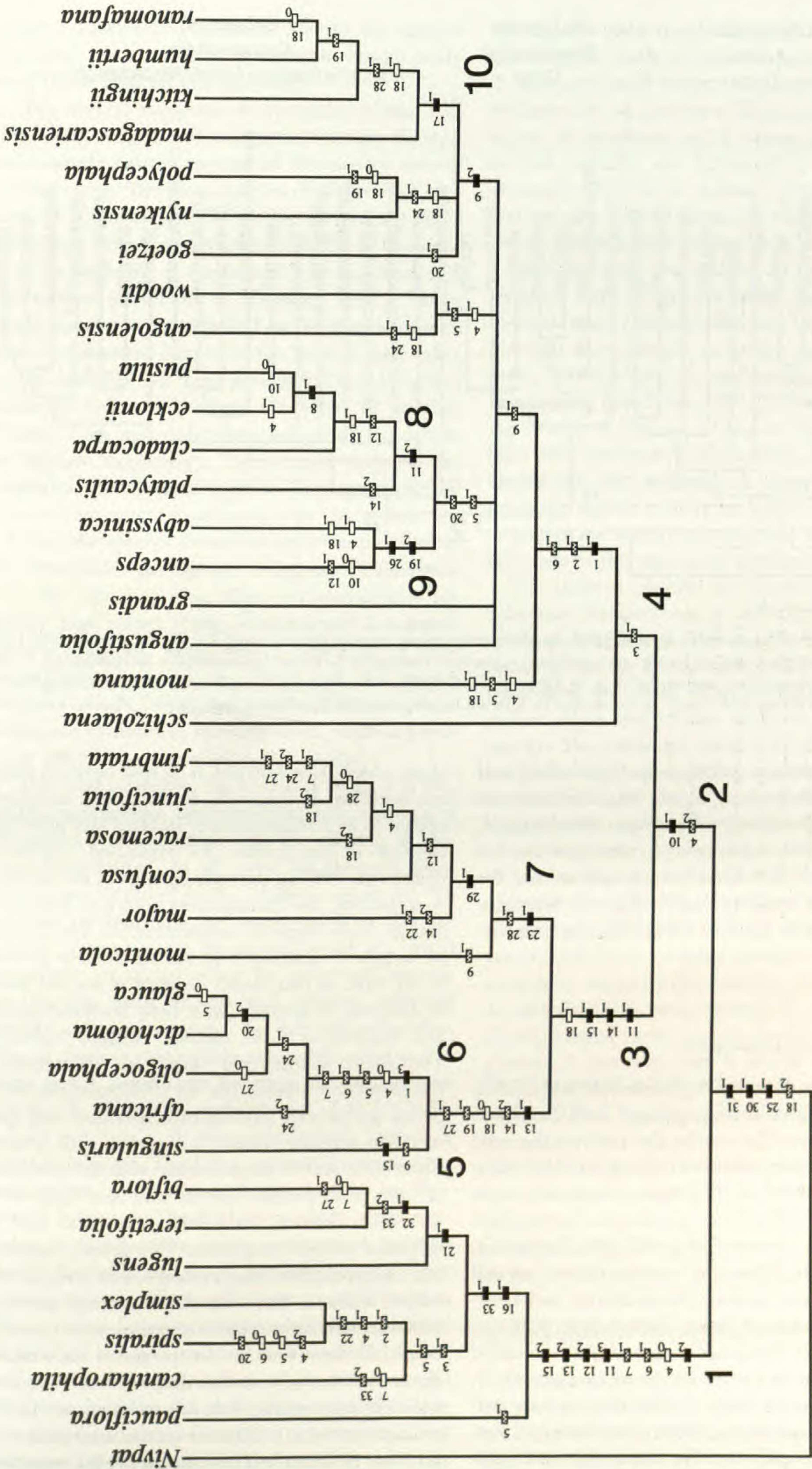
Figure 48. One of 24 trees obtained using the matrix in Table 2 and successive weighting and the mh* and bb* options of Hennig86, showing character distribution (consensus tree shown in Fig. 47B). Numbers opposite the bars on the tree correspond to the character numbers in Table 2; bar shading; solid color = change to the apomorphic state; clear = reversal to the plesiomorphic state (e.g., loss of a specialized condition); stippled = parallel character changes. Taxa were randomly rearranged 15 times with the same result being obtained.
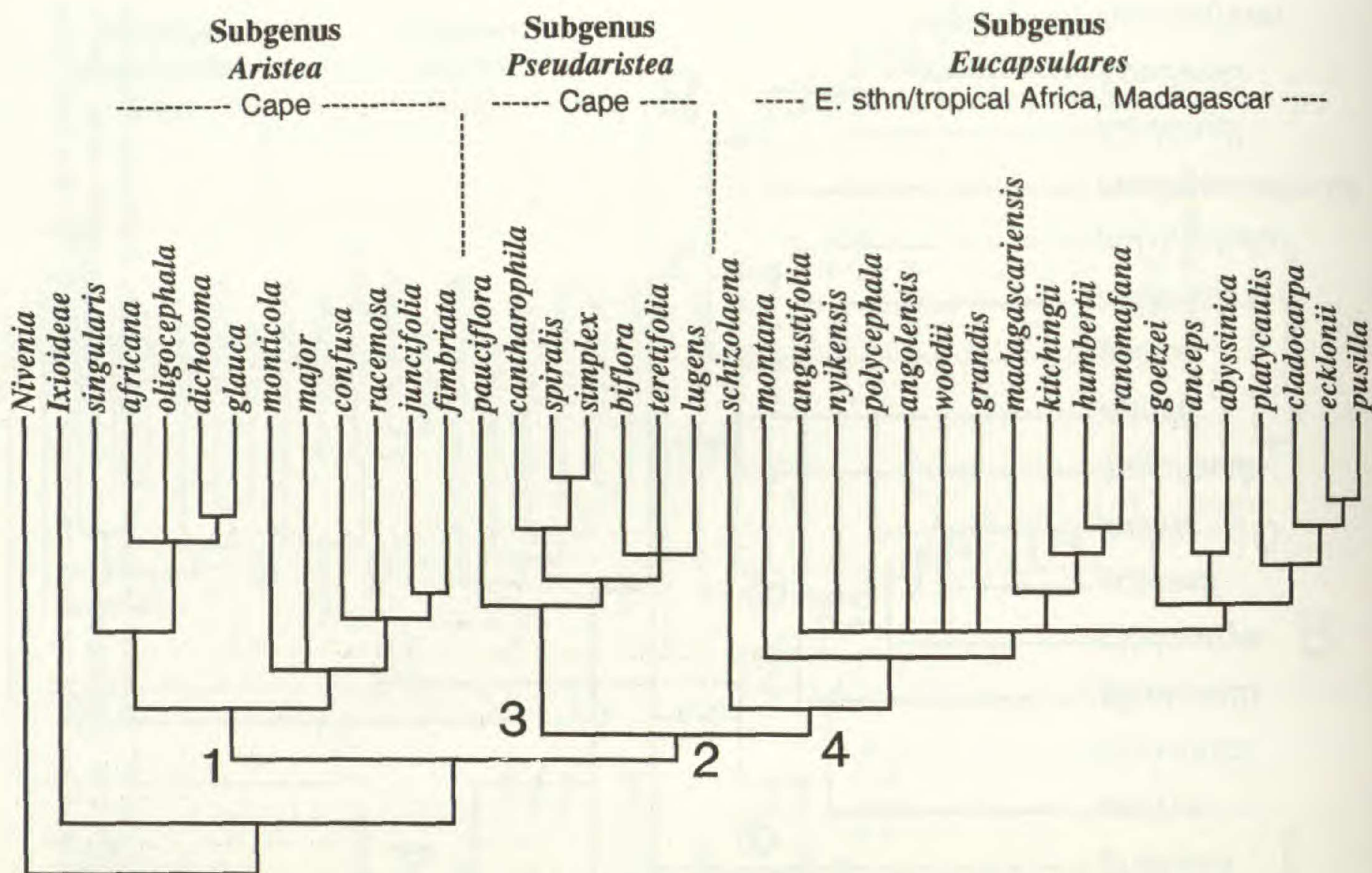
Figure 49. Strict consensus tree of 1012 equally parsimonious trees obtained using the matrix that included the extra taxon, Ixioideae, and using the mh* and bb* options of Hennig86, followed by successive weighting (CI = 45, RI = 80). The same three major clades as in Figure 47B and 48 are present, but the positions of subgenera *Africana* (clade 1) and *Pseudaristea* (clade 2) are shifted in relation to subgenus *Eucapsularis* (clade 3).

compared with their positions in Figures 47B and 48. Within clade 4 of Figure 49 *A. schizolaena* again assumes its isolated position, *A. ecklonii*, *A. pusilla*, *A. cladocarpa*, and *A. platycaulis* are a clade, but now link basally to *A. goetzei* and the two species of section *Ancipites*. The four Madagascan species with porose anthers also remain a single clade.

DISCUSSION

INFRAGENERIC CLASSIFICATION

The results of the phylogenetic analysis confirm the monophyly of *Aristea*, assumed in Material and Methods, above. The results also indicate the need for substantial revision of Weimarck's (1940) infrageneric classification. We propose subgeneric status for the three main clades present in the weighted trees we have generated (Fig. 47B, 49). Preserving, where possible, Weimarck's nomenclature, we call these subgenera *Aristea*, *Eucapsulares*, and *Pseudaristea*. The first of these, clade 3 (Fig. 47B), includes three of Weimarck's sections, *Aristea* (called by him *Cyaneae*) at node 6, *Racemosae* at node 7, and *Singulares* at node 5. The first two are evidently monophyletic and their constitution is supported by the analysis. The third, section *Singu-*

lares, which is monotypic, is nested between these two sections. It does not, as Weimarck assumed, appear to be a taxonomically isolated and primitive member of the genus. As explained elsewhere (Goldblatt, 1995a), the only species of the section, *A. singularis*, was incompletely known to Weimarck and in some respects misunderstood. We hesitate to include *A. singularis* in section *Aristea* (it falls at the base of that clade) because of its odd array of features. It accords with both sections *Aristea* and *Racemosae* in its narrowly winged capsules. The small stature and divaricate inflorescence match section *Aristea*, but the plesiomorphic small pollen grains with monosulcate apertures and apomorphic rugulose exine correspond with section *Racemosae* and contrast starkly with the trisulcate or even more complex grains with reticulate exine of section *Aristea*. On balance, it seems best to maintain section *Singulares*. The unique rounded, and dorsiventrally compressed seeds with a collapsed chalaza, funicular elaiosome, and pendent inflorescence units certainly represent an assemblage of unique features for the genus and support the recognition of a section despite its being monotypic. It is possible that the monosulcate pollen grains represent a reversal to the ancestral state and that *A. singularis* is actually nested in section

Aristea. Elsewhere (Goldblatt, 1995a) the species has been compared to *A. dichotoma.* Future study may throw light on this question.

The second subgenus we recognize (clade 1 of Fig. 47B), subgenus *Pseudaristea,* contains the type and closely related species of Weimarck's section of that name. Two more species of Weimarck's section, *A. ecklonii* and *A. pusilla,* fall in the third subgenus, and *A. zeyheri,* not included in the analysis, is probably a specialized species of section *Racemosae* (Goldblatt & Manning, 1997). These three species were included by Weimarck in section *Pseudaristea* largely on the basis of their elongated capsules. All three have different pollen morphology from the other members of section *Pseudaristea* and differ morphologically in details of capsule morphology. The elongate shape of the capsules, the character used by Weimarck to define his section, must be assumed to be convergent. Including the species described since the publication of Weimarck's monograph, subgenus *Pseudaristea* has just seven species. Their synapomorphies include large pollen grains, extraordinary 2-zonasulculate apertures, exine with a reticulum of very large lumina, on the one hand, and the unique leathery-woody, elongate, tardily dehiscent capsules and cylindrical, truncate seeds combined with long inflorescence spathes on the other.

The third subgenus, *Eucapsulares* (clade 4 of Fig. 47B), incorporates the remaining four sections of Weimarck's classification plus the residue of section *Pseudaristea,* in all some 24 species, 19 of which are included in the cladistic analysis. The species relationships are poorly resolved and our results do not support the recognition of any formal taxonomic groupings within the subgenus. Instead, we suggest using an informal solution, referring simply to "species groups" for well-defined clades. One of these is particularly noteworthy. *Aristea ecklonii* and *A. pusilla* are linked to the Madagascan species *A. cladocarpa* (sole species of sect. *Cladocarpa*) and then to *A. platycephala* (sole species of sect. *Trilobatae*). The latter, an eastern South African endemic, was assigned its own tribe by Weimarck because of its distinctive short, warty capsules. It is otherwise fairly similar to *A. ecklonii* morphologically, and its position on the same clade is not surprising. We suspect that one more species, the southern Cape *A. ensifolia,* which is confined to forested habitats, will fall in this clade too, but pollen is so far unavailable and the species could not be included in the phylogenetic analysis. *Aristea ensifolia* also has elongated capsules, but they are unusual in being indehiscent. The relatively

soft capsule walls simply decay with age, gradually releasing the seeds around the parent plants.

A second small clade, the *Aristea anceps* group, includes the two species of Weimarck's section *Ancipites, A. abyssinica* and *A. anceps* (a third, *A. alata,* will probably also fall here). A common synapomorphy with the *A. ecklonii* group, compressed and broadly winged stems, is the reason the two groups are linked in Figure 49 in a single clade.

Another clade that appears in the successively weighted trees of both analyses, the *A. madagascariensis* group, includes the four Madagascan species that have apically dehiscent anthers, *A. humbertii, A. kitchingii, A. madagascariensis,* and *A. ranomafana* (Goldblatt, 1991, 1995b). The remaining species of Weimarck's section *Eucapsulares* exhibit little evidence of relationship. Species not included in our analysis, *A. compressa* and *A. gerrardii,* appear to us to be fairly closely allied to *A. angolensis,* and we are confident that they would fall close to this species in phylogenetic analyses.

The isolated position of *Aristea schizolaena* in subgenus *Eucapsulares* is difficult to explain in terms of morphology. The species is sister to the remainder of the *Eucapsulares* clade, and its basal position is the result of its having plesiomorphic pollen grains the sulcate apertures of which are smooth. The remaining species have sulculate pollen grains with more complex apertures (disulculate or zonasulculate) always covered with irregularly shaped exine masses. The apparently plesiomorphic pollen grains may represent a reversal, but an alternative position for *A. schizolaena* would result in longer (less parsimonious) trees. The remaining species of the subgenus have sulculate pollen grains, with more complex apertures covered with irregularly shaped exine masses. Morphologically, *A. schizolaena* is unexceptional. It appears to be closely related to the eastern southern African *A. grandis, A. montana,* and *A. woodii* and is readily confused with *A. woodii.* We are reluctant to ascribe any taxonomic significance to the basal position of the species.

The remaining species of subgenus *Eucapsulares* form a residual group that includes the type species of section *Eucapsulares, A. angolensis.* We suggest referring to these species as the *A. angolensis* group.

PHYTOGEOGRAPHY AND PHYLOGENY

There is an extremely close correlation between the phylogeny (and the revised classification based on the phylogeny) and geographical distribution (Fig. 50). All three sections of subgenus *Aristea* oc-
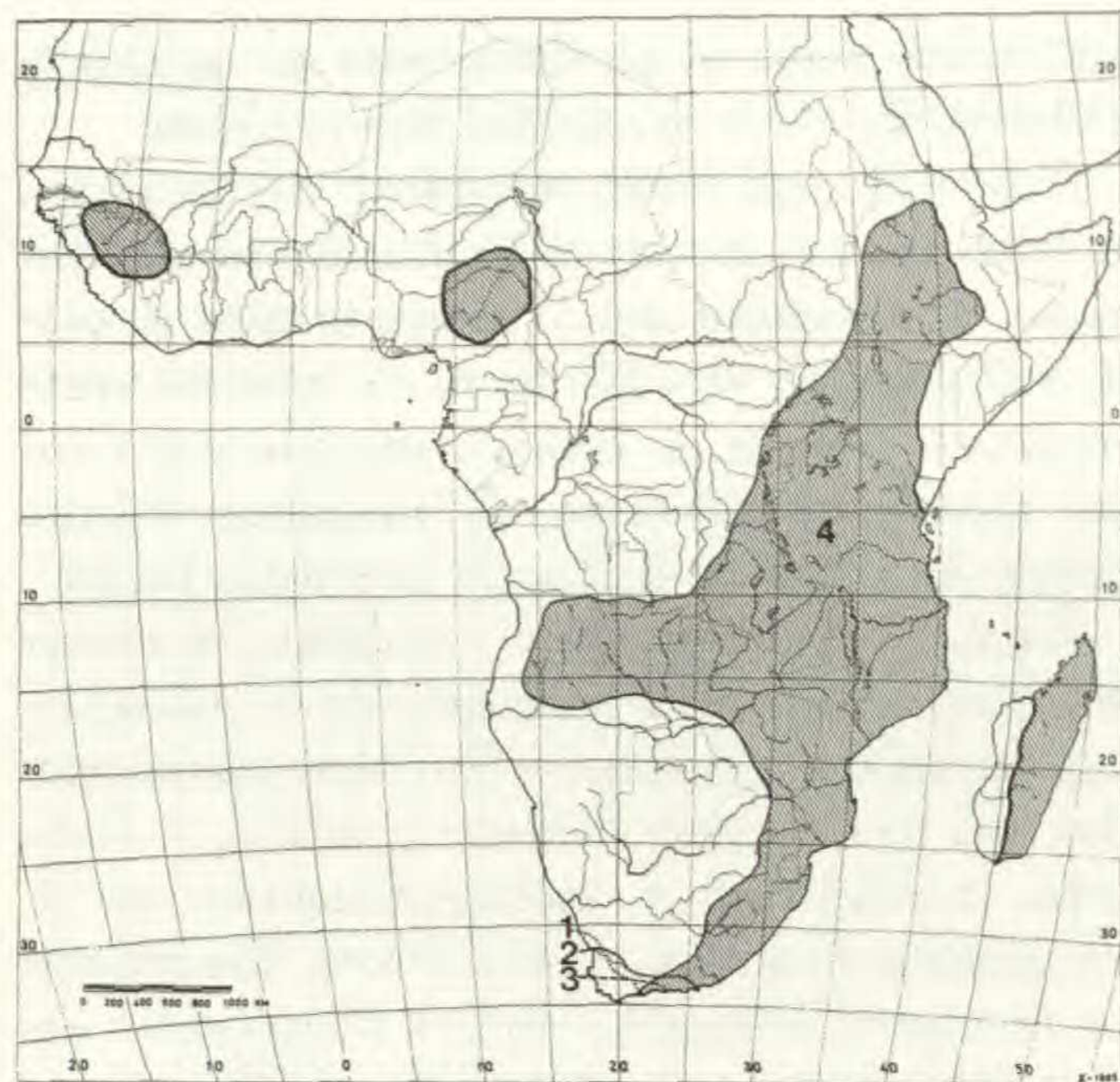
Figure 50. Africa and Madagascar showing the distribution of infrageneric taxa of *Aristea.*—1. Section *Aristea* of subgenus *Aristea.*—2. Section *Racemosae* of subgenus *Aristea.*—3. Subgenus *Pseudaristea.*—4. Subgenus *Eucapsulares.* The Cape Floristic Region nearly corresponds to the range of section *Racemosae* (2).

cur in the winter rainfall climate zone of southern Africa, the Cape Floristic Region (Bond & Goldblatt, 1984) and southern Namaqualand to the north, a part of the Greater Cape Flora Region. With the exception of one species (or two, depending on taxonomy), members of the subgenus are actually restricted to the southwest of the region. Only *A. confusa* and *A. bakeri* (if that species is separate from *A. confusa*) extend eastward to abut the main range of subgenus *Eucapsulares.*

All the species of section *Pseudaristea* also occur in the southern African winter-rainfall zone, thus within the Cape Floristic Region proper. Again, species concentration is highest in the west, repeating the pattern in sections *Aristea* and *Racemosae* of subgenus *Aristea.*

The geographical distribution of subgenus *Eucapsulares* is far wider, extending across all of sub-Saharan Africa and Madagascar. Species diversity exhibits a pattern fairly typical for predominantly temperate-adapted taxa of fewer species as one moves equatorward. There are 14 species of the section in the southern African summer-rainfall zone (including Lesotho, southern Mozambique, eastern South Africa, and Swaziland), of which seven are endemic there. Seven species occur in the Flora Zambesiaca Region (including Malawi, northern Mozambique, Zambia, and Zimbabwe) plus southeastern Zaire. Species endemic to this region plus adjacent southwestern Tanzania include *A. nyikensis* and *A. polycephala.* There are eight spe-

cies in East Africa-Ethiopia, of which *A. alata* is endemic to the wetter highlands of Kenya, northern Tanzania, and southern Ethiopia. A second species, *A. goetzei,* until recently thought to be endemic to Tanzania, is now considered conspecific with the Madagascan *A. nitida,* a later name (Goldblatt, 1996a). Just three species occur in West Africa, none endemic there (unless *A. djalonis* A. Chev. ined., currently included in *A. angolensis,* is recognized). Distribution patterns of more widespread mainland tropical African species of *Aristea* are also informative. The non-endemic species of each of the broad tropical African regions circumscribed above are shared with southern Africa or, in the case of *A. goetzei* with Madagascar, and never with the adjacent region of tropical Africa alone. Thus, *A. abyssinica* and *A. ecklonii* both extend from the contact zone between the South African summer- and winter-rainfall zones northward to Ethiopia and with isolated populations in the highlands of Cameroon. *Aristea angolensis* has a somewhat wider range, extending from eastern southern Africa to Ethiopia in the north and Senegal in West Africa.

Madagascar has seven species of *Aristea,* six of which are endemic. Only *A. goetzei* is shared with southwestern Tanzania. These endemics include species of at least two clades and possibly three (the phylogenetic position of *A. angustifolia* is uncertain). Thus it appears that *Aristea* has colonized Madagascar at least three times from ancestral stock on the African mainland, a notable departure from the usual pattern of African Iridaceae, which are otherwise poorly represented on that island (Goldblatt, 1991, 1994).

BIOLOGY AND ADAPTIVE RADIATION

About the remarkable diversity of pollen types in *Aristea* very little can be said, and nothing conclusive. Pollen variability does not seem to be correlated with any aspect of floral ecology or habitat. Floral presentation in *Aristea* is remarkably uniform. Except for microscopic details of the style branches, flowers of most species seem to be for all intents and purposes identical. The similarity extends even to phenology. Flowers typically open shortly after sunrise and collapse and deliquesce in the early afternoon. Pollination of species with these flowers is, as far as known (Goldblatt & Manning, 1997), by pollen-collecting female bees of the families Anthophoridae, Halictidae, and as is often the case in Africa, *Apis mellifera* (Apidae).

The only exceptions to this pattern are three (possibly five) species of section *Pseudaristea* that appear to be adapted for pollination by beetles

(Scarabaeidae: Rutilinae: Hopliinae), a strategy evidently unique to the winter-rainfall region of southern Africa (Goldblatt & Manning, 1996 and unpublished). These species have flowers that open in mid morning, last until late afternoon, and are pale blue, mauve, or cream with dark contrasting markings. One additional species of the section, *A. spiralis*, is pollinated by long-tongued flies (*Philoliche*: Tabanidae) (Johnson, 1992; Goldblatt & Manning, 1997), but at least *A. pauciflora* of the section has the plesiomorphic pollination syndrome of the genus (Goldblatt & Manning, 1997). Yet all species of the section have virtually the same type of specialized pollen.

We surmise that climate may be a factor with regard to pollen aperture in the section. The winter-rainfall and summer-dry climate is one that is particularly stressful to plants, many of which flower after the wet season and when atmospheric aridity is high and desiccating winds frequent. Drying of delicate floral parts including stigmatic surfaces and pollen grains may put reproductive success at risk. Pollen grains with germination grooves or pores not restricted to one surface of the grain may be an adaptive advantage under such circumstances, once they are transported to a receptive stigma. Two-zonasulculate, trisulcate, or spiraperturate grains like those of sections *Africana* and *Pseudaristea* are more likely to have an aperture in direct contact with the moist stigmatic surface than monosulcate grains with the aperture restricted to one surface. Perhaps it is no accident that the most peculiar pollen grains in *Aristea*, if not in the entire Iridaceae, occur in species restricted to this particular climate zone. In this respect we note that the subfamily of Iridaceae that has radiated most prominently in this region also has unusual pollen for the family, the monosulcate aperture almost invariably having an operculum (Goldblatt et al., 1991).

It must be noted, however, that not all the species of the southern African winter-rainfall region have specialized pollen grains. Apparently plesiomorphic grains characterize all the species of sections *Racemosae* and *Singulares*, and this pollen type is barely represented in the genus outside the winter-rainfall region. In regard to the peculiar sulculate grains with the apertures largely obscured by exine fragments that characterize species of section *Eucapsulares*, we can offer no suggestion of its adaptive value.

Unusual floral features such as tepal markings and elongate anthers, restricted to some species of section *Pseudaristea* (e.g., *A. biflora*, *A. cantharophila*, *A. lugens*, *A. teretifolia*), are evidently directly related to their pollination system. Hopliine beetles are attracted to dark markings on a pale background, and although they are successful pollinators, they also forage on pollen. The larger anthers of species of the section evidently compensate for some loss in pollen by the production of more grains. In *A. spiralis* secretion of nectar and its particularly long stamens are similarly a direct adaptation to a pollination strategy, in this case to long-tongued fly pollination. The flies are nectar feeders, and the long filaments are necessary to permit placement of the pollen-bearing anthers sufficiently distant from the nectar source that they brush against a foraging insect's body as it feeds.

Variation in capsule and seed morphology, so conspicuous in *Aristea*, seems more amenable to evolutionary speculation. High wind velocities are common in the southern Africa winter-rainfall zone at the time when capsules ripen, exposing the seeds. Flattened seeds are more likely than small rounded or angular ones to offer sufficient wind-resistance to be blown some distance away from the parent plant. We suggest that the flattened seeds of species of subgenus *Aristea* are simply adapted for wind dispersal. In the case of *A. singularis* of the subgenus, the rounded seeds with an elaiosome must be dispersed by ants, a strategy well known in the winter-rainfall zone of southern Africa (Bond & Slingsby, 1983; Linder, 1985). We assume that this is a novel adaptation in a subgenus in which the flattened seeds are evidently adapted to wind dispersal. *Aristea singularis* grows in rather sheltered sites such as in the lee of rocks and in shade where wind dispersal is unlikely to operate effectively.

The elongate, leathery-woody, tardily dehiscent capsules of section *Pseudaristea* suggest another strategy for survival in the southern African winter-rainfall zone. Flowering occurs from September to November in the various species, but the seeds are not shed for at least six months after ripening and thus are held in the hard-walled capsules until the rainy season, which begins in April or May. The capsules decay under wet conditions and then release their seeds at a time most favorable for germination. The tough capsules presumably serve as protection from both desiccation and insect predation during the long period that the seeds are retained.

We suggest that these alternative strategies for survival, seed dispersal and/or pollination in different lineages explain to some extent the peculiar adaptations of pollen apertures, flower coloring, anther enlargement, and seed morphology that have permitted species in different lineages of *Aristea* to survive and radiate in the comparatively hostile en-

vironment in the southern African winter-rainfall zone. In this tiny area, less than 1% of the entire range of the genus, there are 28 species of *Aristea* (25 of them endemic), belonging to two subgenera, one with three sections. The only species of the remaining subgenus, *Eucapsulares*, that occur in the winter-rainfall zone are *A. ensifolia* and *A. pusilla*. Both occur in the more mesic southern part of this zone, the former restricted to moist forest or streamside habitats.

Radiation of subgenus *Eucapsulares* clearly follows highland areas in both southern and tropical Africa as well as Madagascar, where it is restricted to areas of relatively high rainfall. The species do not exhibit any particularly striking adaptations in their reproductive morphology. Elongated capsules are restricted to some species of forest or forest margin habitats. It is not clear why the production of more seeds per capsule should occur in this habitat. Eastern southern African and tropical African species show very discrete habitat preferences. Open grassland, short grassland, marshland, and forest each harbor particular species. Except for some species of forested habitats that have elongate capsules, there appear to be no gross morphological or reproductive correlates. Radiation in subgenus *Eucapsulares* thus appears largely habitat-driven.

To put the above observations in perspective, we restate the extraordinary degree of variation in pollen characters in this genus of only moderate size. This variation equals or even exceeds the range of variation found across all the remaining ca. 1700 species of Iridaceae. Much larger genera, including *Gladiolus* (ca. 255 species) and *Moraea* (ca. 130 species), for example, are constant for aperture type and show limited size and exine sculpturing variation (Schulze, 1971a; Goldblatt, 1996b; Goldblatt et al., 1991; Goldblatt & Le Thomas, 1992b). Only *Iris* (ca. 220 species) comes close to *Aristea* in having a range of aperture types and moderate variation in exine patterning (Schulze, 1971b). Why pollen should be so variable in *Aristea* remains ultimately puzzling. Part of the reason may lie in the geological age of the genus. We suspect that it is one of the oldest genera of the family, most likely of pre-Tertiary age. Time alone may have allowed variation in pollen apertures and exine patterning to accumulate, and ultimately to be selected for during periods of climate change such as the establishment during the Pliocene of semiarid and ultimately Mediterranean climate at the southwestern extremity of the African continent.

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APPENDIX 1. Discussion of morphological characters and their polarization and division into character states. Numbers refer to sequence of the character in the matrix.

1–9. Discussed fully in main text.

10. Prominent rhipidial spathes that enclose the entire inflorescence including the floral bracts, the ancestral state, characterize all genera of the outgroup excepting a few specialized species of *Nivenia*. Within *Aristea* most species have short rhipidial spathes that partially enclose the inflorescences so that the buds and floral bracts are not concealed, the derived state. The floral bracts are usually as long as or longer than the spathes in these species.

The exception: species of section *Pseudaristea* have large rhipidial spathes that exceed the floral bracts and conceal the buds.

11. Capsules of the outgroup are rounded in section or barely three-lobed. Derived broadly winged capsules (sects. *Aristea* and *Racemosae*) are scored as 1 and deeply 3-lobed capsules (sect. *Pseudaristea* and a few species of section *Eucapsulares*) are scored as 2. The states are regarded as unordered.

12. Capsule shape in profile is treated as a separate character from shape in transverse section (character 11). Most species of the outgroup have capsules more or less ovoid and up to twice as long as wide. [The elongate, fusiform capsules of one genus of the outgroup, *Patersonia*, are probably specialized owing to their inclusion in the spathes.] Oblong capsules 3–4 times as long as wide are scored as 1, and extremely elongate capsules more than 5 times as long as wide (all species of sect. *Racemosae*) are scored as 2. The character states are additive and hence treated as ordered.

13. Capsules are cartilaginous to nearly woody and loculicidally dehiscent for at least one-third their length in the outgroup genera as well as in most species of section *Eucapsulares*. Capsules of section *Aristea* are cartilaginous with particularly thin lateral walls of the wings and dehiscent only near the apices and often partially along the septa as well. These capsules are scored as 1. Capsules are incompletely known in *A. singularis* but appear to conform to type 1 and are so scored. Species of section *Pseudaristea* have leathery to woody, tardily dehiscent to indehiscent capsules, scored 2. The character states are treated as unordered.

14. Seed number is largely independent of capsule length. Seed number per locule is few (usually one) in the outgroup genera *Klattia*, *Nivenia*, and *Witsenia* but several to many in *Patersonia*. We score the outgroup as ? for this character. Most species of *Aristea* have several to many seeds per locule. Several species of section *Racemosae* typically have four seeds per locule, scored 1, and some have two (or one) per locule, as do all species of section *Aristea*, scored 2. The states are additive and treated as ordered.

15. Rounded to segmental (prismatic) seeds are the most common type in *Aristea* and in the entire family. *Patersonia* has seeds of the same type, scored as 0, but *Klattia*, *Nivenia*, and *Witsenia* have tangentially flattened, shield-shaped seeds, unique in Iridaceae (Manning & Goldblatt, 1991). Radially compressed seeds characterize sections *Aristea* and *Racemosae*, scored 1. The more or less cylindric seeds with truncated or oblique ends are scored as 2, and the globose, vertically compressed, arillate seeds of *A. singularis* are scored 3. The character states of seed shape are treated as unordered.

16. Anthers are relatively short and oblong in the outgroup genera and most species of *Aristea* as well. Species of section *Pseudaristea*, except *A. pauciflora*, have linear anthers, regarded as derived.

17. Longitudinal anther dehiscence is plesiomorphic in Iridaceae and is the usual condition in *Aristea*. Four Madagascan species have apomorphic apically dehiscent anthers (Goldblatt, 1991, 1995b).

18. When flowering stems have more than just one terminal inflorescence the lateral inflorescences are borne on short branches (or occasionally long branches in the outgroup). In some species of *Aristea* at least a few of the lateral inflorescences are sessile, and sometimes the normal condition is for all lateral inflorescences to be sessile.

It seems useful to distinguish two states, some lateral inflorescences consistently sessile (1), or all normally sessile (2). The character is additive and hence is regarded as ordered.

19. The arrangement of individual inflorescence units is highly variable in Nivenioideae. The ancestral condition is most likely racemose (Goldblatt, 1993), with lateral inflorescences borne on short lateral branches (sessile lateral branches, thus spicately arranged, are considered homologous). Species of section *Aristea* have the inflorescences arranged dichotomously, scored 1. *Aristea abyssinica* and *A. anceps* have one or two inflorescence units crowded at the stem apex, scored 2. The character states are unordered.

20. The outgroup genera have lightly compressed or terete flowering stems, and this is the condition in most species of *Aristea*. A few isolated species have strongly compressed, more or less two-winged flowering stems (ancipitous sensu Weimarck, 1940), including *A. spiralis* (sect. *Pseudaristea*) and *A. abyssinica, A. alata, A. anceps, A. cladocarpa,* and *A. platycephala* (sects. *Ancipites, Cladocarpae,* and *Trilobatae* of Weimarck). In *A. dichotoma* and *A. glauca* the upper part of the flowering stem is also compressed, but the stems are narrow and only obscurely winged. The two states are scored as 1 and 2, respectively, and are treated as unordered.

21. Most species of *Aristea* as well as those of the outgroup genera have the inner tepal whorl similar to the outer in length and color (flowers of *Patersonia* have very short to vestigial inner tepals, clearly apomorphic for that genus). Only *A. lugens* and *A. teretifolia* have the outer tepals substantially smaller than the inner and differently colored.

22. Flowers are more or less upright in the outgroup and all but two species of *Aristea*. Only *A. simplex* and *A. spiralis* have secund flowers that face to the side.

23. Styles of Nivenioideae range from minutely notched apically, broadly lobed apically, or divided into slender recurved arms. The pattern in the outgroup is confusing and we prefer to score the outgroup as ?. In *Aristea* most species have lobed and fringed style branches, scored 0, and a few species, all section *Racemosae*, have the styles minutely notched apically, scored 1.

24. The rhipidial spathes, and usually the floral bracts, are green to brownish and chartaceous in the outgroup. A few species of *Aristea* have the spathes and bracts pale, scarious and either semitransparent, scored 1, or opaque, scored 2 (Table 2). The character states are regarded as unordered.

25. Septal nectaries are present in all genera of the outgroup (Goldblatt, 1993; Rudall, pers. comm.). Species of *Aristea* do not produce nectar, thus lack nectaries, except for *A. spiralis*, which has perigonal nectaries (J. C.

Manning, pers. comm.). Absence of nectaries is regarded as derived.

26. The ancestral condition in Iridaceae, including nearly all species of *Aristea*, is a flowering stem bearing a few leaves decreasing in size above. A few species, including *A. abyssinica* and *A. anceps* (Table 2), have a flowering stem consisting of one long basal internode and bearing a short subterminal bract-like leaf.

27. A low, cushion-like growth form is rare in Iridaceae and not present in the genera of the outgroup. Species of section *Aristea* and *A. singularis* may be described as forming low, cushion-like tufts with the flowering stems often not raised much above the leaves.

28. Few to several inflorescence units (or only one) per flowering stem are plesiomorphic in the outgroup genera. Stems with many inflorescence units are a conspicuous feature of a few species (Table 2), notably *A. major* and *A. confusa* (sect. *Racemosae*).

29. Seed surfaces in the outgroup genera typically have primary sculpturing (Manning & Goldblatt, 1991), as do most species of *Aristea*, the surface usually being more or less rugose (unpublished data), treated as the plesiomorphic condition. Seeds of species of section *Racemosae* examined (Table 2) lack primary sculpturing and are treated as derived.

30. Species of the outgroup have leaves with a strand of sclerenchyma below the margins (Rudall & Burns, 1989), but all species of *Aristea* examined for the character lack subepidermal marginal sclerenchyma (Rudall, 1995; J. Manning, pers. comm.), regarded as a derived condition (0).

31. A perianth tube is present in all genera of the outgroup and is presumably plesiomorphic for Nivenioideae. All species of *Aristea* have the tepals united basally in a vestigial tube, 1–2 mm long, scored as 1.

32. Tepals of the outgroup and most members of the ingroup have tepals symmetric about the midvein. The inner tepals are conspicuously asymmetric about the midvein in *A. biflora* and *A. teretifolia*, thus apomorphic for tepal symmetry.

33. The ancestral flower color in Nivenioideae is most probably blue (present in all *Nivenia*, all but one species of *Patersonia*, most species of *Aristea*). A few species of subgenus *Pseudaristea* have pale blue flowers, but three species have cream to mauve flowers (Table 1). Flower color is treated as an unordered multistate character, blue (0), pale blue (1), mauve to cream (2).

Additional character when Ixioideae is included in the analysis:

34. Flowers lasting at least one day and not deliquescing on fading characterize *Klattia, Nivenia, Witsenia,* and all Ixioideae. Flowers of *Aristea* last less than one day (usually fading just after midday) and deliquesce on fading, the derived state.